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THE EPIDEMIOLOGY AND CONTROL OF DOWNY MILDEW ON HOPS

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ABSTRACT

THE downy mildew caused by *Pseudoperonospora humuli* is the most destructive disease of hops *(Humulus lupulus)* in New York, its economic control being a primary requisite for successful hop production in this State. The problems of its epidemiology and control vary greatly under different seasonal and regional conditions. The purpose of this investigation has been to gain a better understanding of the various environmental factors as they affect the development of the fungus and of the disease and to use this knowledge in developing economic control measures.

The fungus attacks all parts of the plant except the roots. Young tissues are very susceptible and are often systemically invaded. The killing of stems, blossoms, and cones greatly reduces the quality and quantity of the crop.

Hops are the only host of the mildew fungus in this State. The fungus lives over the winter in the soil as oospores which are produced in diseased parts of the plant thruout the growing season. Summer spores (sporangia) are produced on infected plant parts thruout the season during night periods of high humidity.

Both oospores and sporangia germinate to form zoospores which infect the plant when water is present for at least 2 hours. Cool to moderate temperatures (13° to 18° C) are best for sporulation, germination, and infection by the mildew parasite. Such temperatures, combined with frequent rains, dews, and fogs, provide ideal conditions for rapid increase in disease.

Downy mildew can be economically controlled on susceptible varieties even in the most epidemic years by following a program of sanitary practices and *thoro* spraying. Homemade bordeaux mixture and Yellow Cuprocide are the more effective of the materials tested.

Bordeaux 6–4–100 or Yellow Cuprocide 1½–100 should be applied (a) when the vines are about 8 feet high, (b) 2 weeks later, (c) at the start of the bur period, and (d) at the start of cone formation. More frequent applications including an earlier spraying are necessary in valley yards. Dusting two or three times during August with copper-lime 25–75 or Cuprocide-sulfur 7–93 is necessary to protect the cones if any new spikes or diseased leaves are present at that time.

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INTRODUCTION

THE downy mildew fungus, *Pseudoperonospora humili* (Miy. and Tak.) Wilson, was first reported in 1906 from Japan (35).[1] In 1909 Davis (8) found the disease on native wild hops in Wisconsin. It was observed in England during 1920 (52) and its introduction or discovery in all other European hop-growing countries followed within a few years (5, 7, 9, 26, 31, 37, 43). Since its discovery in the Pacific Northwest in 1928, the disease has assumed epidemic proportions in many of the hop-growing regions of the Pacific Coast.

Downy mildew of hops was first observed in New York State in 1928. The disease became very prevalent in many hop yards which were established after 1933. Central and Eastern New York hop growers who did not spray in succeeding years have experienced a loss of at least one-third of their crop in the average year. In fact, the losses in quantity and quality have become so serious that hops can no longer be grown successfully in this State unless control measures are developed and put into practice.

Investigations have been directed toward determining the conditions under which the causal fungus lives over from one season to the next, the part that weather plays in the infection of the host, how infection spreads from plant to plant, and the value of various fungicides at different critical periods. Such studies have been in progress at Geneva and at Waterville, N. Y., since 1936. The findings and the recommendations based thereon are reported in this bulletin.

LABORATORY AND GREENHOUSE STUDIES

GERMINATION EXPERIMENTS WITH SPORANGIA, OOSPORES, AND ZOOSPORES

TEMPERATURE AND NUTRIENT RELATIONS

Sporangia.—The effect of temperature upon germination of sporangia was determined by the technic of McCallan (33). The spor-

[1] Figures in parenthesis refer to Literature Cited, Page 45.

angia were suspended in cold water, diluted to 28,000 per cc, and placed at the desired temperature within 20 minutes. At the end of the incubation period, the sporangia were killed with formaldehyde. The percentage of germination was determined in at least four microscopic fields chosen at random from each drop. At least 150 spores were counted on each of the duplicate slides used in each test.

Sporangia held at 24°, 20°, 15°, and 10° C began to germinate after 1, 1¼, 1½, and 2 hours, respectively (Fig. 1). They completed the liberation of swarm spores at these temperatures in 1½, 2, 2½, and 4 hours, respectively. The optimum temperature was between 15° and 20° C as previously reported by Arens (1). Germination was observed at temperatures as low as 5° C. Fewer of the sporangia germinated at 24° than at the lower temperatures. Spores germinated in only one of three trials made at 28° C.

Sporangia released zoospores equally well in double-distilled water and in dilute solutions of sugars, mineral salts, orange juice, and in hop leaf decoctions.

Oospores.—Oospores were obtained from diseased stems, leaves, cones, and seedlings after they had overwintered under natural con-

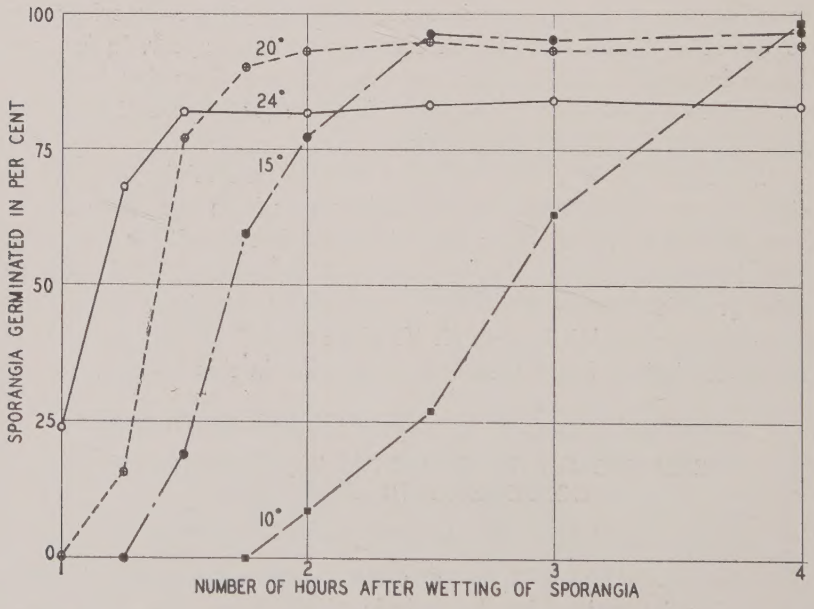

FIG. 1.—THE GERMINATION OF SPORANGIA OF *P. humuli* IN RELATION TO TEMPERATURE AND PERIOD OF WETTING.

ditions. These were germinated in the supernatant liquid taken from water suspensions of soil. Germination occurred at temperatures from 5° to 20° C after wetting periods of 4 to 16 days. Observations on the occurrence and germination of oospores are described by other workers (1, 6, 14, 24, 43, 59).

Zoospores.—Zoospores began to germinate in 2½ to 3½ hours at 15° to 24° C. The incubation period was reduced to about 1 hour by placing pieces of hop leaves in the water with the spores. The germ tubes grew toward the leaf tissue.

Germination of zoospores in distilled water was erratic and sparse. Better germination occurred in the more concentrated suspensions and in suspensions to which calcium citrate or a hop leaf was added. Germination was inhibited in 0.01 per cent orange juice and in 0.425 per cent sodium chloride solution.

Zoospores suspended in water immediately exploded when the suspension was diluted with a large volume of water. Young or old and washed or unwashed hop leaves added to spore suspensions helped to keep the zoospores from bursting, prolonged their activity, and stimulated them to germinate.

LONGEVITY OF SPORES

Sporangia.—Hop leaves bearing mature sporangia were held in open dishes in refrigerators at 5°, 10°, and 15° C, in the laboratory (18° to 24° C), and in the greenhouse at summer temperatures (20° to 35° C). A calcium chloride desiccator was used in the laboratory in addition to the open dishes to hasten drying. The sunlight in the laboratory was diffused, while in the greenhouse it was direct. There was no light in the refrigerators. At the beginning of the tests and after various periods of drying, sporangia were removed from the leaves and tested for germination (Fig. 2).

The time required for sporangia to germinate increased directly with increase in age, as reported by Zattler (59). Older sporangia required 3 or 4 hours of wetting at an optimum temperature to germinate.

After the longer periods of drying, concentrated suspensions of the sporangia were tested for viability by inoculation on greenhouse plants. In every case, viable sporangia infected young hop leaves.

Sporangia rapidly lost their viability at the conditions of laboratory and greenhouse temperature, humidity, and light (Fig. 5). About 10 per cent of the spores were viable after 9 days, and practically all were

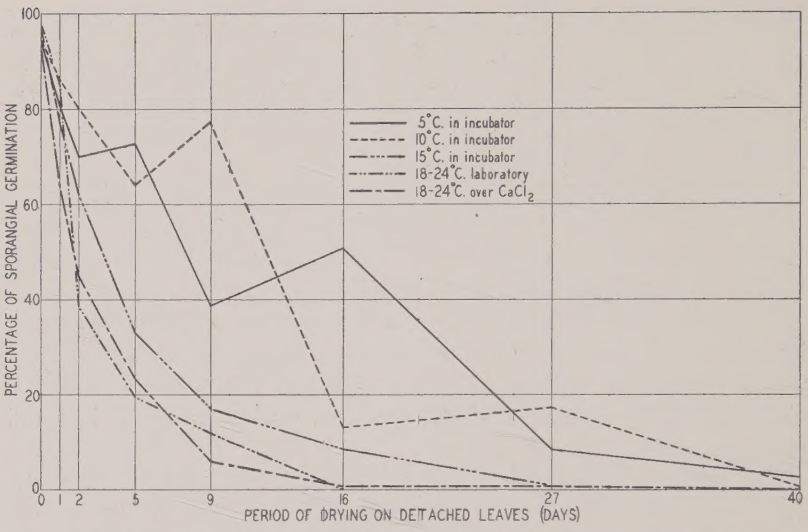

FIG. 2.—LONGEVITY OF SPORANGIA OF *P. humuli* ON DETACHED HOP LEAVES IN OPEN DISHES.

dead at 16 days, while at 5° and 10° C, some spores were still viable after 40 days. The sporangia lived only a few hours when separated from their host plant and dried on glass slides in the laboratory.

The following test indicates further that some sporangia survive severe drought for at least 4 weeks. This conclusion is supported by the results of other workers (1, 5, 25, 59).

The viability of spores on a young plant in the field was determined at intervals during the period July 31 to September 1, 1939. Moisture was excluded from the plant. All the sporangia under test had matured prior to July 31 because the weather during August was so hot and dry that further sporulation was prohibited. The percentage germination on July 31 was 78; August 4, 86; August 11, 65; August 18, 32; August 25, 10; and September 1, 4.

Zoospores. — The maximum period of motility heretofore reported for zoospores has been about 24 hours (1, 25). In the following tests, they remained active for several days. Sporangial suspensions used to obtain the zoospores were made by two methods, *viz.*, (a) by atomizing the leaf with a minimum amount of distilled water, and (b) by soaking the leaves in distilled water for 15 minutes. The sporangia were held in suspension at 20° C until they germinated. In diluted suspensions prepared by the first method, zoospores remained motile for but a few hours at temperatures of 10° to 20° C and little germina-

tion took place. However, when a living hop leaf was added to similar suspensions, the zoospores remained active for as long as 5 days at 10° and 2 days at 20° C, and many of them germinated. In suspensions prepared by the second method, zoospores survived for 1 day at 10° and for several hours at 20° C.

Rather paradoxically, macerated hop leaves added to the suspensions proved slightly toxic to the zoospores.

Oospores.—Oospores germinated only after a dormant period of several months and they survived 2½ years of dry storage in the laboratory and a similar period at −18° C.

INFECTION EXPERIMENTS WITH SPORANGIA

MATERIALS AND METHODS

Potted plants of the variety Millstate (12) were grown from rhizome cuttings in the greenhouse at 64° to 78° F (18° to 26° C). Only two shoots were allowed to develop and these were inoculated when they had six to eight pairs of leaves. A suspension of young sporangia (less than 1 day old) containing about 56,000 spores per cc was sprayed on the leaves by means of a DeVilbiss atomizer until it began to run off. The plants were then placed in the saturated atmosphere of a moist chamber for 20 hours.[2]

The number of lesions per square inch on the most severely infected part of each leaf was counted 6 to 8 days after inoculation.

RELATION OF TEMPERATURE AND WETTING PERIOD TO INFECTION

The effect of temperature and length of moist treatment on infection was tested between March 27 and April 21, 1939. Plants, inoculum, and conditions of inoculation and incubation were uniform for the series. Two tests were made at 10°, 13°, 18°, and 24° C. After each time interval four plants were removed from the inoculation chamber, placed before a fan, dried off within 15 minutes, and returned to the greenhouse.

The shortest periods necessary for infection at 24°, 18°, 13°, and 10° C were 1½, 2, 4, and 6 hours, respectively (Fig. 3). The heaviest

[2]In experiments which did not require temperature control, plants to be inoculated were placed under tap-water sprinklers of the type used in retail stores to keep vegetables fresh. Excellent infection was obtained under these atomizers in several different types of inoculation experiments with hop mildew. A burlap enclosure protected the plants from the effects of excessive air movement.

infection occurred on plants incubated for 24 hours at 13° and 18° C.

Temperatures higher than 24° C were not used since they seldom or never occur during infection periods under field conditions. The use of temperatures lower than 10° C would have been desirable. In the field, infection has been known to occur at air temperatures as low as 5° to 6° C.

The specific time required for zoospores to germinate and set up infection was not determined. This period may be approximated closely for any given temperature, however, by taking the difference between the shortest time required for infection when leaves were inoculated with sporangia (Fig. 3) and the shortest time required for liberation of the swarm spores from the sporangia (Fig. 1). Thus, the lapse of time between germination of sporangia and initiation of infection on the leaf, including the 15 minutes necessary to dry the leaves before a fan, may be deduced as ¾ hour at 24° C, 1 hour at 18° to 20°, 2¾ hours at 13° to 15°, and 4¼ hours at 10°.

Maximum infection was secured in tests where fresh sporangial suspensions were placed directly on the leaf. When the same suspensions were held until zoospores had been produced before inoculation, only about half as many lesions were produced. Apparently the zoospores lose vigor within the short period before inoculation, or else

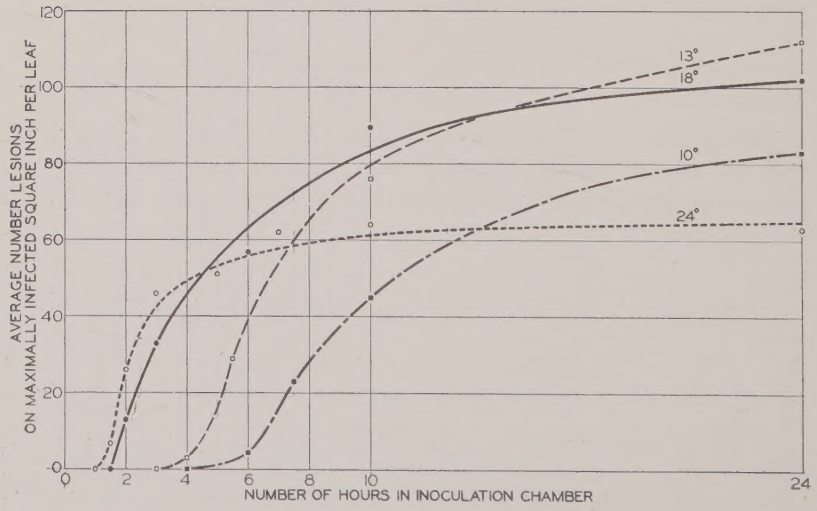

FIG. 3.—THE RELATION OF TEMPERATURE AND WETTING PERIOD TO ZOOSPORANGIAL INFECTION OF POTTED MILLSTATE HOP PLANTS BY *P. humuli*.

contact with the leaf tissue stimulates either the sporangia or zoospores.

LONGEVITY OF SPORANGIA ON INOCULATED LEAVES

The effect of desiccation on the longevity of sporangia sprayed on the host was determined by placing plants inoculated with a sporangial suspension in sunlight on a greenhouse bench for various intervals before they were transferred to a moist chamber where conditions were ideal for infections. The drying was very destructive to the sporangia. Few lesions developed after 12 hours of exposure and none after 24 hours (Table 1).

TABLE 1.—EFFECT OF DESICCATION OF SPORANGIA ON LEAVES OF MILLSTATE ON THEIR ABILITY TO PRODUCE LESIONS.

DURATION OF DESICCATION, HOURS*	PERIOD IN MOIST CHAMBER, HOURS†	AVERAGE NUMBER OF LESIONS PER SQUARE INCH PER LEAF
0	16	Over 150
4	20	57
8	16	26
12	16	14
24	16	2
38	16	0

*On greenhouse bench at 50 to 70 per cent relative humidity and 19° to 24°C. Spores were sprayed on the leaves at 8 a.m.
†Inoculation chamber held at 20°C and 100 per cent relative humidity.

AGE OF LEAF IN RELATION TO SUSCEPTIBILITY

The youngest tissues of the hop plant always proved to be the most susceptible to infection. During July and August, older leaves and stems as found in the field have been much more difficult to infect than growing tissue.

Hop leaves attained their resistance to mildew infection more rapidly with higher temperatures (Table 2). Eight uniform potted plants, 20 days old, that had grown at 65° F (18° C) from rhizome cuttings were divided into two equal lots, one of which was left at 65°, the other being removed to a greenhouse in which the temperature averaged 76° F (24.5° C). After 4, 10, 21, and 35 days, one plant from each greenhouse was inoculated with sporangia. The leaves of the plants in both houses became more resistant with increase in age, but after the tenth day, the leaves at 76° became progressively more resistant than those at 65°.

TABLE 2.—CHANGE IN SUSCEPTIBILITY OF LEAVES OF MILLSTATE* AS THEY AGE AT DIFFERENT TEMPERATURES.

PERIOD OF CONDITIONING, DAYS	NUMBER OF LESIONS ON LEAVES CONDITIONED AT	
	65°F	76°F
4	119	128
10	91	87
21	51	17
35	37	8

*A selection of "English Cluster", the name of two or more varieties which were standard in New York for many decades.

EFFECTIVENESS OF FUNGICIDE APPLIED BEFORE AND AFTER INOCULATION

Bordeaux 4–2–100 and rosin-lime-sulfur 3–6–100 gave protection when applied 1 day before inoculation but were relatively ineffective in checking the development of the disease when applied 6 hours after inoculation (Table 3).

Rosin-lime-sulfur tended to suppress sporulation on plants held under bell jars (Table 3), as shown by Yarwood (56). However, the sulfur material had little effect on sporulation when the plants were placed under sprinklers in the greenhouse. In the field, rosin-

TABLE 3.—EFFECT OF BORDEAUX 4–2–100 AND ROSIN-LIME-SULFUR 3–6–100 ON INCIDENCE OF INFECTION AND SPORULATION BY *P. humuli* WHEN APPLIED AT DIFFERENT TIMES IN RELATION TO THE INFECTION PERIOD.

PLANT NUMBER	NUMBER OF VINES	WETTING PERIOD, HOURS*	TREATMENT		AVERAGE NUMBER LESIONS ON MAXIMALLY INFECTED SQUARE INCH PER LEAF	LESIONS SPORULATING, PER CENT†
			Material	Before or after inoculation		
1	2	20	None	———	94	97
2	1	20	None	———	97	—
3	1	20	None	———	113	—
4	2	20	Bordeaux	1 day before	0	—
5	3	20	Rosin-L.S.	1 day before	0	—
6	2	6	None	———	72	99
7	2	6	Bordeaux	6 hrs. after	39	42
8	2	6	Rosin-L.S.	6 hrs. after	21	11
9	2	20	Bordeaux	20 hrs. after	89	35
10	2	20	Rosin-L.S.	20 hrs. after	78	5

*Inoculation chamber held at 21°C and 100 per cent relative humidity.
†Counts made on four representative leaves after plant was placed under bell jar to force out sporangia.

lime-sulfur inhibited sporulation only slightly. Sulfur dust completely prevented sporulation under bell jars at 72° to 76° F (22° to 24.5°C), but only slightly inhibited sporulation under the atomizers.

FIELD STUDIES

SEASONAL RECORDS OF DISEASE AND WEATHER

The seasonal development of the downy mildew disease was followed during the five seasons from 1937 to 1941 by determining every 6 to 14 days the percentage of infected leaves and shoots on unsprayed plants of the Millstate variety in two experimental yards. The leaves counted were within 7 feet of the ground.

Records pertaining to temperature, humidity, rainfall, infection periods, sporulation periods, the first appearance of sporangia on spikes, disease development on leaves and vine tips, and dates of spray applications, made as needed to control the disease in experimental yards, are given in Figs. 4 to 8 and in Table 4. The periods of wetting recorded as infection periods are only those of sufficient duration, as determined in the greenhouse (Fig. 3), to permit infection at the given temperature. These periods are indicated as the total hours of wetting from the rainfall of any 24-hour period, ending at 8 a.m. of the day of recording.

DEVELOPMENT OF EPIDEMICS

HOP CULTURE IN RELATION TO DISEASE DEVELOPMENT

The intensive nature of hop culture and the concentration of yards in certain localities encourage the development and persistence of diseases such as downy mildew. Hops are grown in permanent yards

TABLE 4.—MONTHLY MEAN AND AVERAGE TEMPERATURES FOR THE HOP-GROWING SEASON AT WATERVILLE, N. Y., 1936–41.

YEAR	MAY		JUNE		JULY		AUGUST*	
	Mean†	Av.‡	Mean	Av.	Mean	Av.	Mean	Av.
1936	57.3	56.9	67.8	68.2	72.3	73.4	70.8	72.5
1937	54.7	54.0	63.5	63.3	68.3	67.0	69.7	69.8
1938	53.4	52.7	65.8	62.8	69.8	68.3	70.0	71.5
1939	57.0	56.4	63.9	62.3	67.0	67.5	69.3	69.9
1940	54.9	55.0	61.6	61.3	67.2	66.7	64.7	64.7
1941	55.7	55.7	66.5	66.2	71.0	70.3	65.4	64.1

*First three weeks of August only.
†Average of minimum-maximum readings taken at 8 a.m.
‡Thermograph average (13) obtained by integrating the temperature curves with a planimeter.

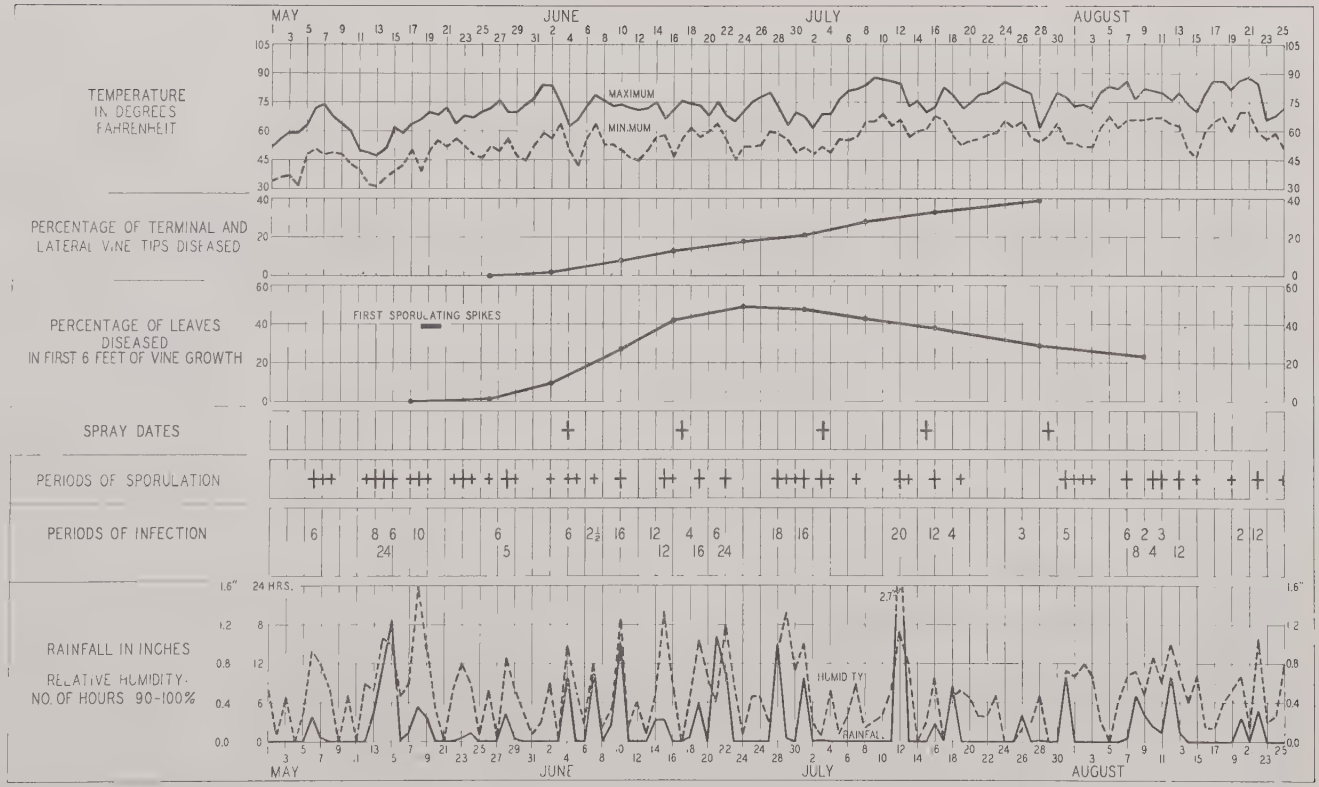

FIG. 4.—SUMMARY OF CERTAIN EPIDEMIOLOGICAL RECORDS PERTAINING TO THE CONTROL OF DOWNY MILDEW OF HOPS AT WATERVILLE, N. Y., 1937.

Sporulation periods coincident with rainfall are indicated with the larger crosses.

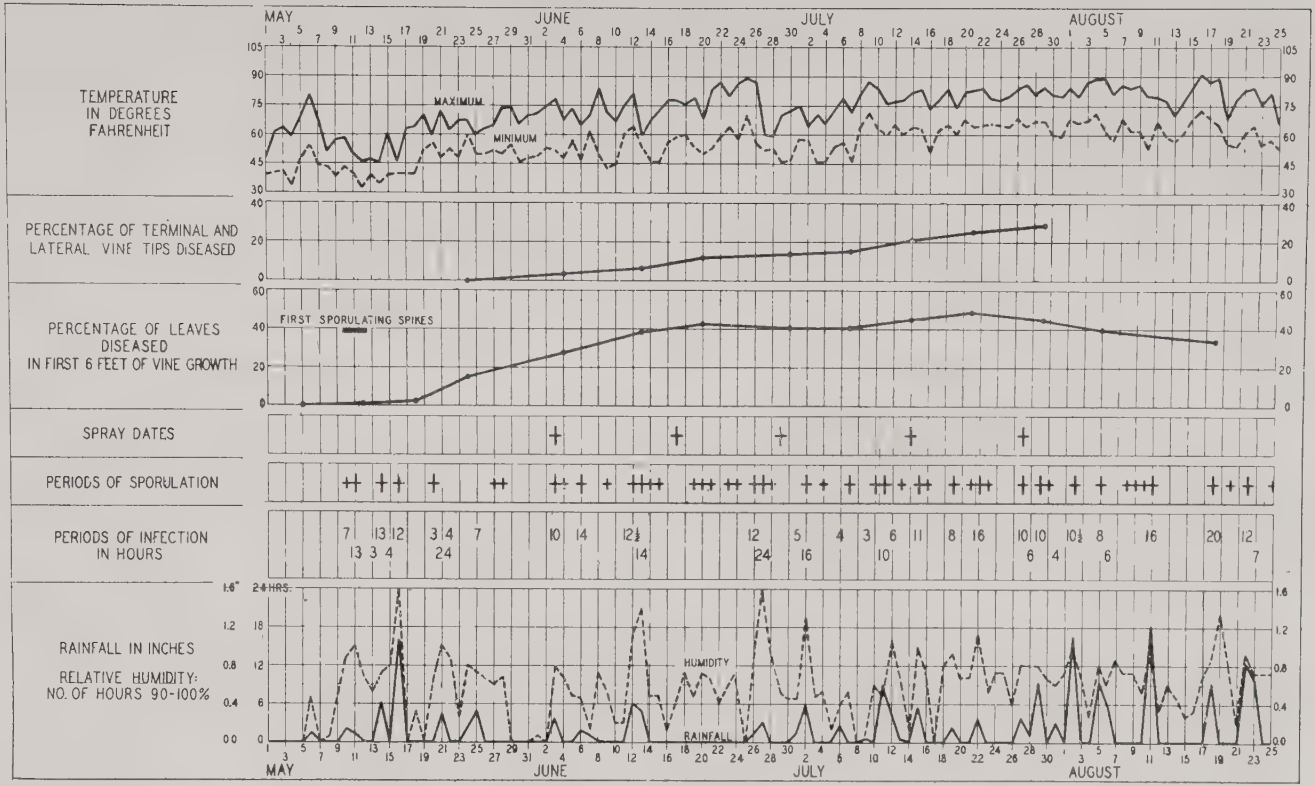

FIG. 5.—SUMMARY OF CERTAIN EPIDEMIOLOGICAL RECORDS PERTAINING TO THE CONTROL OF DOWNY MILDEW OF HOPS AT WATERVILLE, N. Y., 1938.

Sporulation periods coincident with rainfall are indicated with the larger crosses.

FIG. 6.—SUMMARY OF CERTAIN EPIDEMIOLOGICAL RECORDS PERTAINING TO THE CONTROL OF DOWNY MILDEW OF HOPS AT WATERVILLE, N. Y., 1939.

Sporulation periods coincident with rainfall are indicated with the larger crosses.

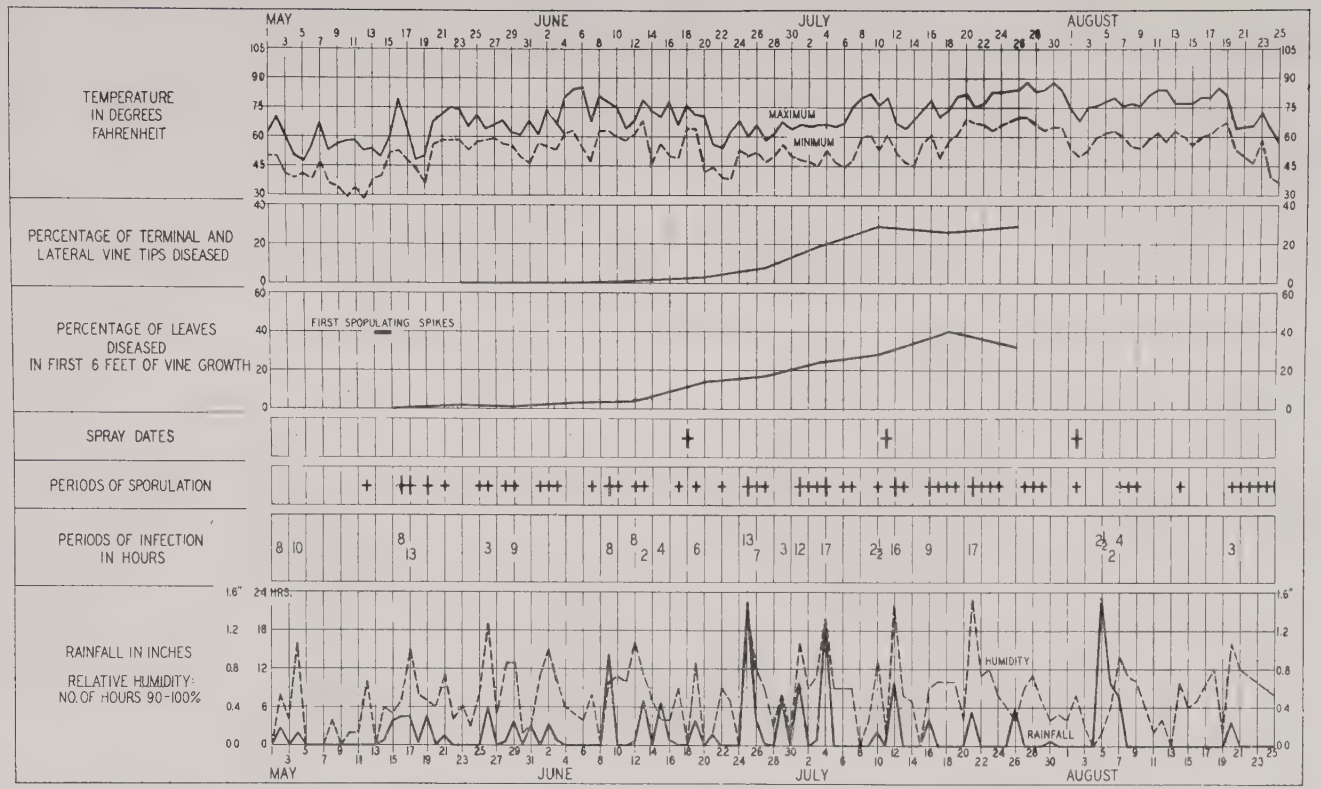

FIG. 7.—SUMMARY OF CERTAIN EPIDEMIOLOGICAL RECORDS PERTAINING TO THE CONTROL OF DOWNY MILDEW OF HOPS AT WATERVILLE, N. Y., 1940.

Sporulation periods coincident with rainfall are indicated with the larger crosses.

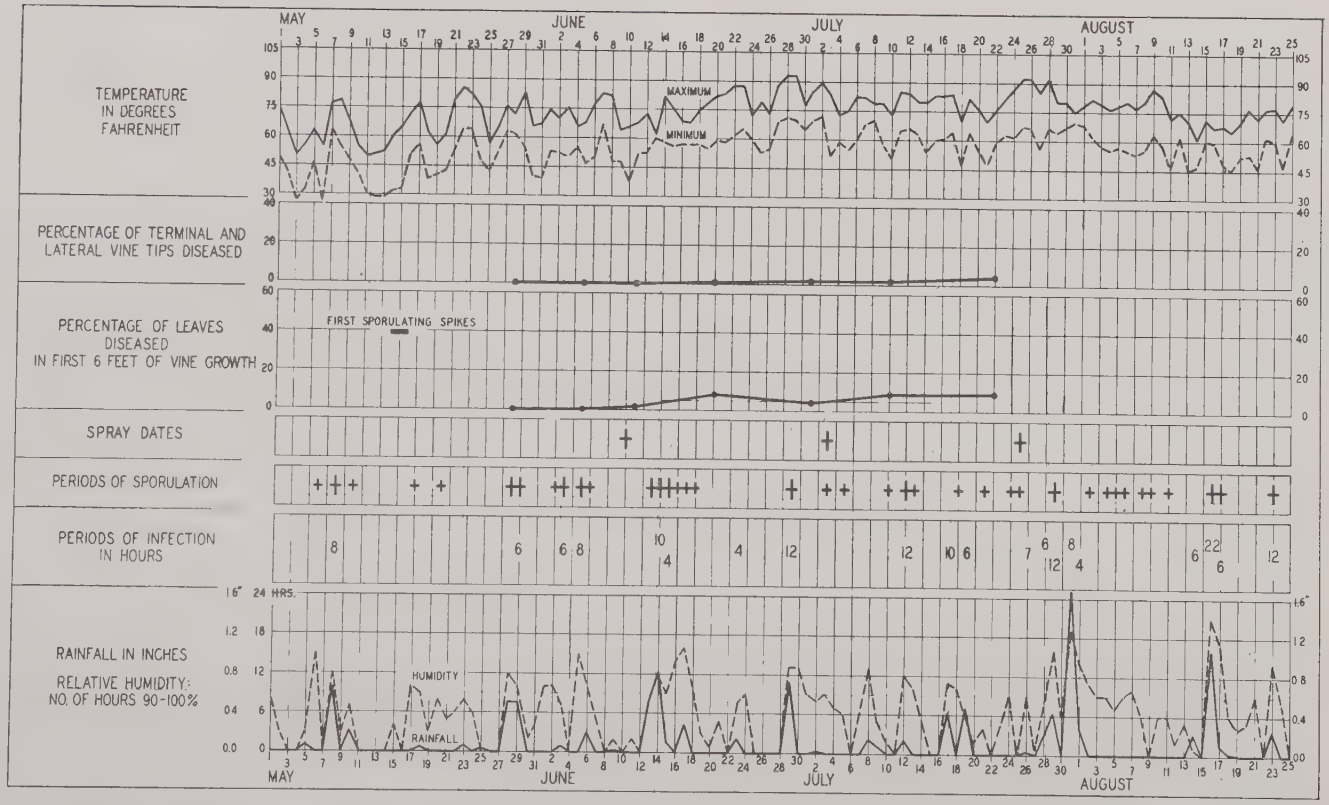

FIG. 8.—SUMMARY OF CERTAIN EPIDEMIOLOGICAL RECORDS PERTAINING TO THE CONTROL OF DOWNY MILDEW OF HOPS AT WATERVILLE, N. Y., 1941.

Sporulation periods coincident with rainfall are indicated with the larger crosses.

since they are perennial plants. During the first season the vines are not tied up so they are on the ground where conditions favor mildew infection. Often they are seriously weakened or even killed by the fungus.

In subsequent seasons, the crown of each hop plant produces several new shoots during May. A few shoots from each plant or hill are selected and trained upon poles or trellises during May and June. The necessary cultural operations involved in the training and stripping of the young vines can rapidly spread the fungus.

The vines make a growth of 20 to 30 feet by the time of flowering in mid-July. They may grow as much as 20 inches in 24 hours, making thoro protection by spraying impractical. Since leaves and cones continue to grow until a week or two before harvesting, there is always considerable new growth exposed to infection.

Early in September each year, the vines are cut off near the ground to facilitate harvesting. This affords an opportunity to clean up the hop yard and reduce the carry-over of disease-producing spores.

DISEASE SYMPTOMS

The symptoms of the downy mildew disease in New York State are much the same as those reported from other hop-producing areas (2, 5, 15, 36, 43, 44, 47, 52). However, some of the symptoms are mentioned here to acquaint the reader with certain terms and concepts.

In the field, symptoms show up on the leaves about one week after infection whereas on stems and cones about two weeks are required. Shoots infected in the meristematic tissue develop rosetted growths that are commonly spoken of as "spikes". They have thick, brittle stems with an excessive development of brown pith tissue, whereas normal or healthy shoots are hollow. Infected shoots

FIG. 9.—BASAL SPIKE ON LEFT AND HEALTHY SHOOT ON RIGHT.

Both shoots grew from rhizome cuttings of the Millstate variety and were planted in downy mildew-infested field soil in the greenhouse on February 9, 1942. Photographed March 17.

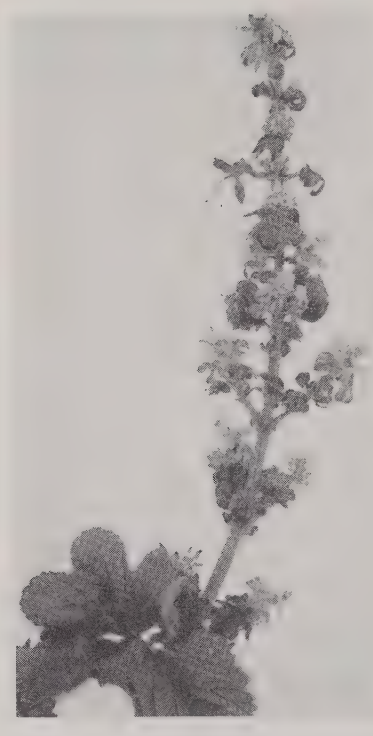

FIG. 10.—A TERMINAL SPIKE, THE RESULT OF SYSTEMIC INFECTION OF THE TERMINAL BUD OF A VIGOROUS HOP VINE BY ZOOSPORANGIA OF *P. humuli.*

The stem is very thick with short internodes and small, cupped, yellowish leaves. Few terminal spikes show lateral growth to the extent that this one does. Photographed June 17, 1937.

appearing directly from the crown in the spring are called basal spikes (Fig. 9) to distinguish them from infections taking place thruout the season on vine tips and axillary buds that are referred to as terminal and lateral spikes, respectively (Fig. 10).

All spikes are systemically invaded. They produce only small, yellowish, downwardly cupped leaves which appear grey or black on their under surfaces after humid nights, when the sporangiophores of the fungus emerge from the leaf stomata. The sporangia appear on the older leaves first. Thus, a succession of spore crops is produced from basal to tip leaves on each spike before it ultimately dies.

Local infections of mature leaves by air-borne spores produce small, angular, pale green, water-soaked lesions. Lesions on young leaves are large and diffuse. In both cases, the spots later become necrotic and dark brown (Fig. 11), after one or more crops of spores have been produced.

The sporangia germinate quite readily in water by producing zoospores. These swimming spores are capable of causing infection on any young hop tissue that is supplied with natural openings.

Sporangia are produced in such profusion that a general epidemic may develop at any time that favorable moisture conditions obtain during the growing season. In addition, oospores develop within all infected tissues thruout the growing season of the hop plant.

HOSTS

Infection by *Pseudoperonospora humuli* of wild hops native to Japan, Europe, and North America is reported to be common (22, 29, 36, 42). Escaped hops are also commonly infected and serve as a source of inoculum for cultivated hops in Europe and North America.

Natural infection of plants outside the genus *Humulus* has not been reported. Nettles (*Urtica urens* L., *U. dioica* L., and *U. lyallii* Wats.) have been inoculated with the hop fungus by several workers (19, 23, 42, 45). These results led to the theory (42) that the hop downy mildew arose as a mutation from the nettle downy mildew *Pseudoperonospora urticae* (Libert) Salmon and Ware. Hoerner (19) succeeded in infecting other members of the nettle family (*Celtis* sp. and *Cannabis* sp. in addition to *Urtica* sp.) with the hop downy mildew. According to other workers (3, 5, 27, 37, 38, 53), however, the nettles are immune to the hop mildew.

One nettle, *Urtica lyallii,* has been found occasionally near hop yards in this State. However, no infection with downy mildew has ever been noted on it. Nettle plants in the field were inoculated with a spore suspension of the hop fungus and covered with glass jars overnight. A few leaf lesions resulted, but did not develop spores.

Infection of wild or escaped hops, apparently plays no important part in the epidemiology of the disease in this State.

OVERWINTERING OF THE FUNGUS

It has not been determined convincingly whether *Pseudoperonospora humuli* overwinters by means of oospores in the soil or by means of the vegetative mycelium within the perennial crown of the hop plant. Some European observers (34, 41, 43, 54, 58) have offered evidence that there is a "perennial mycelium," but others (1, 18, 25, 30, 36) doubt whether such mycelium starts the epidemic in the spring.

Infected shoots and healthy shoots often arise from the same crown or even from the same

FIG. 11.—A HOP LEAF WITH SPORULATING LESIONS OF THE DOWNY MILDEW ON THE UPPER SURFACE (ON LEFT) AND LOWER SURFACE (ON RIGHT).

node on the vine, as pointed out by Arens (1). Hence if infection does originate from mycelium overwintering in the dormant crowns, it is obvious that this mycelium is not entirely or generally systemic. For example, in an isolated yard where infected shoots were removed at weekly intervals during May 1938, 228 of the 411 hills had at least one infected shoot during the period, but only 8 hills had infected shoots all 4 weeks, 46 had them for 3 of the 4 weeks, and 80 for 2 of the 4 weeks. Similar data indicating chance infection were obtained in this same field the following year. This circumstantial evidence strongly suggests that perennial mycelium in the crown is not the major source of infection.

Infection arising from oospores in the soil might be prevented by treating the soil with fungicides, such as the calcium cyanamide suggested by Hoerner (16, 17). Approximately 700 plants were treated with calcium cyanamide during 1937, 1938, and 1939 by uniformly distributing 2 or 4 ounces within a 10-inch radius of the crown of each plant immediately preceding growth in the spring. This soil treatment reduced infection 63 to 82 per cent.

On a ½-acre plot in 1938, infected shoots developed in 48 per cent of the untreated hills and in 10 per cent of the treated hills, but the number of individual shoots infected was much further reduced, from 1.5 to 0.1 per hill by the cyanamide treatment. These results are interpreted as an indication that the treatment protected individual shoots against infection rather than that it sterilized those crowns containing possible perennial mycelium.

Further evidence that overwintering inoculum comes from infested soil rather than from infected crowns was obtained by growing several hundred rhizome and crown cuttings in the greenhouse. Cuttings from infested fields of Late Cluster and "English" Cluster were planted in sterile compost and in mildew-infested field soil. Mildew infection developed only on the cuttings grown in the infested soil; never on those grown in the compost.

In three other tests, rhizome and crown cuttings taken from badly mildewed plantings were surface-sterilized in 0.1 per cent mercuric chloride solution and planted in disease-free soil in the field. Only healthy plants developed. Unsterilized cuttings, grown under the same soil conditions, developed a few diseased shoots, presumably from oospores on the surfaces of the unwashed cuttings. The parent plants left in their infested soil supported about one spike per hill.

All of these tests tend to show that young shoots do not become

infected from previously infected rhizomes or crowns. It seems obvious that under New York conditions the fungus overwinters for the most part as oospores in the soil and that these infect the young shoots as they grow thru the soil.

OCCURRENCE OF PRIMARY INFECTION

The primary infection produced by oospores on young shoots, leaves, and seedlings is not of much economic importance in itself. In general, so few shoots are injured that the yard is not severely affected. The infection is important, however, because it serves as the source of spores that may infect the new growth thruout the yard. Primary infection has been observed in every yard examined during the past few years. The infected shoots are quite conspicuous during May and June in all yards where they are not removed.

Primary infection may be more prevalent in trellised yards, where the vines were not cut off during the previous year's harvest, than in poled yards where the vines were cut off just above the ground line at harvest. In the former case, more growth is exposed to autumn infection. Oospores develop abundantly during the epidemic condidions that prevail in the post-harvest months.

Hop seedling volunteer plants that are common in some West Coast yards become infected and can serve as an important early source of inoculum (23) ; but in New York yards seedlings are uncommon and they are not considered a factor in the epidemiology of the disease.

Leaves near the soil are subject to primary as well as secondary infections. Primary infections of leaves were greatly reduced by the practice of pulling out all untrained vines before they fall over on the soil.

Basal spikes represent the important phase of primary infection in this State. Spikes were first observed early in May of each year within 2 weeks after the first appearance of growth above ground. The first appearance of sporangia on these spikes followed within a few days (Figs. 4 to 8).

The incidence of primary infection, recorded as number of diseased hills, has been found to increase following an epidemic year. Counts of spiked hills were made in six representative yards during May in each year from 1937 to 1940, inclusive. In five of these yards, a lower percentage of hills produced spikes in 1937 than in 1938 or 1939. The lowered incidence of primary infection in 1937 followed the

very dry summer of 1936. The percentage of spiked hills was again lower in 1940, following the dry summer of 1939.

Beard (4) and Salmon and Ware (50) observed an increase in basal spiking following a wet summer and advanced the theory that this was due to the washing of sporangia to the ground by heavy summer rains, followed by systemic infections of the crown. This theory does not fit the evidence obtained in New York, as reported in the preceding section on "Overwintering of the Fungus". As further refutation of this theory, hop rhizomes and crowns that became infected in the unsprayed portions of a New York yard in the wet summer of 1940 were grown in the greenhouse in 1941, but all new shoots from them were healthy. In fact, many of the infected rhizomes and buds on these plants were dead at the time of digging in October or after storage in a cold frame.

All evidence, therefore, indicates that the greater incidence of the basal spike type of primary infection in a spring following a wet summer is due to the increased production of oospore inoculum, not to increased systematic infection of the underground perennial host parts.

PRODUCTION OF SPORANGIA

Sporangia are produced on all infected above-ground parts of the hop plant. The conditions necessary for abundant formation of spores are high humidity, especially at night; a favorable temperature; and the presence of sporulable lesions.[3] Unfortunately for hop growers, these three factors prevail all too often during the hop-growing season in New York. High humidity occurs rather frequently as shown by the fact that in only a few cases during the 5 seasons of 1937 to 1941 did more than 7 days elapse between sporulation periods (Figs. 4 to 8). Field temperatures are nearly always within the range favorable to sporulation. Sporulable lesions were found in every yard examined at any time in each of the 5 years from about May 15 until harvest, even thru the driest midsummer periods.

Then, too, the short period between inoculation and sporulation of 5 to 7 days for leaf lesions and 8 to 16 days for infected shoots as determined in the field makes for a rapid build-up of secondary inoculum.

In tests with excised plant parts, lesions which had supported one

[3]The term "sporulable", as explained by Yarwood (55), means the ability to sporulate.

or more crops of sporangiophores were only feebly sporulable when again placed in moist chambers. Diseased parts left on the host plant, however, have supported successive crops of sporangia. Some of the sporulable lesions on potted hop plants held outdoors produced fresh crops of sporangia on six separate nights during June, 1938, whenever the relative humidity approached 100 per cent for at least 8 hours of the night. This same successive sporulation could take place under ordinary culture.

DISSEMINATION OF SPORANGIA

The appearance of downy mildew in rapid succession in the various isolated hop-growing regions of Europe and North America during the decade starting in 1920 has given rise to the belief that viable spores may be borne on the wind for hundreds of miles (5, 39, 45, 47). Failure to exclude the fungus from certain isolated localities in Europe substantiates this belief.

The following experiments demonstrate that spores are readily disseminated over short distances. Healthy, greenhouse-grown plants of the Late Cluster variety were transferred for a 7-day exposure period to locations near an isolated ½-acre hop yard on June 2, 1938. One plant was placed at each of the following distances from the south-east corner of the planting: 10, 50, 100, 200, and 400 feet. Three other plants were left in the greenhouse as controls. In the yard, approximately 7 per cent of the lower leaves were infected. During the 7 days, a 10-hour infection period occurred on June 2 with 0.25 inch rainfall and a 14-hour period on June 5 with 0.20 inch rainfall. Dew formed on the nights of June 3 and 8. On June 9 the plants were returned to the greenhouse and given a 20-hour moist treatment. After 5 days, the percentage of leaves infected on plants at 10, 50, 100, 200, and 400 feet were 25, 18, 16, 0, and 5, respectively. The controls were not infected.

On June 13, 1938, similar potted plants were placed on four sides and in the middle of the same yard. One plant was placed 12 feet from each corner and two plants in the middle of the yard. No rain fell during the 9-day period. Dew formed on the nights of June 13, 14, 18, 19, and 20. The plants were returned to the greenhouse and given a 20-hour moist treatment on June 22. Downy mildew lesions appeared on 6 per cent of the leaves of the plant that had been located at the northeast corner, on 20 per cent of the leaves on the plant at the southeast corner, on 11 per cent of the leaves on the plant at the

southwest corner, on 2 per cent of the leaves on the plant at the northwest corner, and on 33 per cent of the leaves of the plants that had been located in the center of the yard. The prevailing winds were from the north and west. That viable spores are carried on the wind in dry weather is indicated by the fact that the heaviest infection occurred on the plant placed at the lee side of the yard. A similar observation has been reported by Hoerner (18) in Oregon.

Dissemination of sporangia by air currents would account for the spread of the disease from basal spikes and from lesions on lower leaves upward to the higher parts of the vine. Unquestionably, tho, the greatest amount of infection is brought about by rainfall washing spores from the upper vines to lower leaves, blossoms, and cones. Thus, most epidemic outbreaks are preceded by two phases, *viz.*, (a) the wind dissemination of spores from the first-infected lower parts to the upper parts of the plant, and then (b) the distribution of spores downward from these vantage points by rain.

OCCURRENCE AND ROLE OF SECONDARY INFECTION

All parts of the hop plant except the roots may be attacked as a result of infection by sporangia. The occurrence of secondary infection is recorded graphically in Figs. 4 to 8 and serves as a measure of potential inoculum. Infection of blossoms and cones was not recorded. The latter is more important as a measure of the severity of epidemics rather than as a measure of potential inoculum.

The occurrence of secondary infection depended on the presence of viable sporangia, on susceptible tissue being available, and on suitable infection periods. Of these three factors only the latter was limiting in the production of epidemics. Even when inoculum was scarce, as on June 26, 1938, and August 5, 1940, two or three infection periods spaced a few days apart produced abundant inoculum and, with later rains, severe epidemics followed. New, susceptible tissue in the form of young leaves, stems, blossoms, or cones is produced thruout the season until harvest. Blossoms and cones are especially susceptible, and serious infection of these parts occurred following a relative scarcity of inoculum.

Secondary infection accounted for the major spread of the disease, for the chief injury to the host plant, and for the development of oospores for the next year's primary inoculum.

CONTROL MEASURES

Only preventive measures have proved of worth in controlling the downy mildew of hops. These measures are sanitation, the use of fungicides, and the use of resistant varieties.

During the first few years after the appearance of hop mildew, sanitary measures were the sole control recommended by English workers (43, 44). After the disastrous epidemic of 1927, however, these same experimenters reported that systematic spraying was also necessary (46). On the continent of Europe and in North America, practically all workers have recommended a combined program of sanitation and spraying (10, 15, 21, 36, 49, 58).

SANITATION

The importance of sanitation in New York hop culture has been demonstrated both experimentally and by field incidents. Sanitary measures have proved essential to mildew control in plantings unsuitably located with respect to air drainage and wind sweep. Since it is impossible to keep the rapidly growing shoot tips completely protected with fungicides from one day to the next during May and June, destruction of inoculum by sanitary measures is often necessary to prevent heavy infection of the upper vines and leaves.

The sanitary practice that has been found of greatest aid in mildew control is the roguing of basal spikes before they sporulate. Spikes were removed from one-half of a 3-acre yard on May 3, 10, 16, and 25 and on June 3, 1938. The percentage of vine tips infected in the control and rogued parts, respectively, were for June 4, 1.3 and 0.4; for June 14, 3.7 and 1.1; and for July 18, 8.4 and 3.8. No fungicides were used. Still more striking results were obtained in 1938 and 1940 when comparisons were made between different yards, using one as a control and the other for spike removal. The wind dissemination of spores within a yard neccssitates elimination of spikes from the whole yard in order to bring out the full effects of spike sanitation.

Frequent roguing of spikes during May and early June of 1938 delayed the onset of serious secondary infection and made it possible to postpone the first spray application for several days. In the dry season of 1939 spike sanitation carried the plants safely thru the month of June and the first half of July without the added protection of spraying.

Removal of spikes was found to be most necessary in yards with little air drainage. In epidemic years in such yards some of the crop

was lost in spite of early and frequent spraying when the spikes were not removed regularly during May and June. On the other hand, in epidemic years any measure of fungus eradication and disease control attained thru sanitary practices was quickly overcome when the hop plants were not protected by a fungicide. Sanitary practices alone did not protect the crop in the epidemic years of 1937, 1938, and 1940.

Besides the removal of basal spikes, certain other sanitary measures were of value, *viz.*, (a) elimination of leaves and extra growth at the base of the plants by the practices of "stripping" the vines and "suckering"; (b) removal of terminal and lateral spikes; (c) treatment of the soil over crowns with calcium cyanamide (see section on "Overwintering of the Fungus", page 19); (d) fall clean-up of yards; and (e) elimination of escaped hops to the greatest practicable distance.

SPRAYING AND DUSTING EXPERIMENTS

Bordeaux mixture has been widely recommended in the control of hop downy mildew (2, 15, 28, 30, 36, 37, 40, 47, 48, 49, 51, 60). Other spray materials have been proposed, mostly on the basis of their being less injurious to the hop plant, such as cuprous oxide (30), copper oxychlorides and cuprenox (11), rosin-lime sulfur (56), and zinc sulfate plus lime (21). The addition of cottonseed oil to bordeaux increased its retention by the plant and reduced plant injury (30, 32, 51). The use of spreaders with bordeaux is deemed unnecessary by most workers, but spreaders are recommended on the West Coast (2, 15, 20, 21, 36, 56). Dusting with cooper-lime has been reported by Hoerner (15) to be an uncertain control measure but helpful as an adjunct to regular spraying practices in large plantings.

It was desired in the experiments reported here to find the lowest concentration of the most effective spray materials and the minimum number of applications that would afford adequate protection. Bordeaux was used as the standard spray for comparison with other fungicides.

The experiments were conducted in several commercial yards and in two experimental yards in the vicinity of Waterville, N. Y., from 1936 to 1941.

MATERIALS AND METHODS

The plants were sprayed by power equipment and guns using pump pressures of 350 to 400 pounds. For large-scale applications vertical booms were used instead of hand-directed guns. Two nozzles from a

broom and one orchard gun were fixed to a ½ inch pipe mounted on either side of the sprayer tank. The guns at the top of the pipes were 3 feet above the tank and could be lowered when necessary to prevent the breaking of vines. Spraying with guns was carried out to the point of dripping. When using the booms, the sprayer was operated in each row at 2 to 3 miles per hour. Sprays were applied with guns at the rate of 200 to 400 gallons per acre and with fixed nozzles at the rate of 150 to 200 gallons per acre.

Records on disease were obtained in the week preceding harvest. The percentage of cones attacked by downy mildew was determined from random samples of at least 300 cones for each treatment, the cones being picked in the area of 6 to 10 feet above the ground.

SEASONAL CONDITIONS AND RESULTS

Data on several spray tests made during the period 1936 to 1941, inclusive, are presented in Table 5. The benefits from spraying were measured by the percentage of cones infected and the yield of marketable cones.

1936.—The temperature range was unusually high and rainfall scanty thruout this season. A moderate amount of infection was present on young shoots and leaves until the middle of June, after which little further infection occurred. The crop was seriously reduced by drought but remained disease-free. As a consequence, the fungicide tests had little significance and are not included in Table 5.

1937.—This season was characterized by moderate temperatures and excessive rainfall, especially in June. The onset of secondary infection was somewhat retarded by the late appearance of basal spikes, but unusually frequent infection periods in June (Fig. 4) caused an early and severe disease development. Dry, warm periods at the beginning and end of July checked the disease to quite an extent. The infection periods of the second week of August brought about moderately severe cone infection.

Bordeaux and Cuprocide gave the best control in the 1937 tests (Table 5). The other copper compounds, zinc oxide, and zinc sulfate plus lime were less effective. The addition of spreaders to Cuprocide reduced both disease control and the yield. Apparently, the spreaders reduced the tenacity of the Cuprocide. Bordeaux and zinc oxide caused leaf injury. This injury was markedly reduced by the addition of cottonseed oil to the spray mixtures. The oil increased the effectiveness of bordeaux and Cuprocide, probably by causing greater retention and tenacity of the copper materials.

TABLE 5.—SUMMARY OF RESULTS OF SPRAYING AND DUSTING EXPERIMENTS FOR THE CONTROL OF HOP DOWNY MILDEW, ONEIDA COUNTY, N. Y., 1937–1940.

YARD NO.	SPRAY MATERIALS[a]	APPLICATIONS[b]	NUMBER OF PLANTS	CONES AND BURS INFECTED, PER CENT	YIELD PER ACRE, LBS.[c]
		1937			
11[d]	Zinc oxide 4–100	3, 5, 7, 8	35	9	1,020
	Zinc oxide 2–100	3, 5, 7, 8	34	14	1,090
	Zinc oxide 2–100 plus CSO ¼ per cent	3, 5, 7, 8	34	5	1,110
	Bordeaux 8–8–100	3, 5, 7, 8	35	2	1,275
	Bordeaux 4–4–100	3, 5, 7, 8	32	3	1,225
	Bordeaux 4–4–100 plus CSO ¼ per cent	3, 5, 7, 8	33	1	1,340
	Cuprocide 2–100	3, 5, 7, 8	34	2	1,350
	Cuprocide 1–100	3, 5, 7, 8	32	5	1,175
	Cuprocide 1–100 plus CSO ¼ per cent	3, 5, 7, 8	32	4	1,263
	Nonsprayed, between spray plots[e]	———	337	57	695
	Nonsprayed, in adjacent rows	———	640	72	520
2	Copper Hydro "40" 8–100	2, 3, 4, 6, 7	32	7.3	834
	Cupro K 6–100	2, 3, 4, 6, 7	33	17.2	700
	Cuprous sulfide 2–100	2, 3, 4, 6, 7	31	15.7	680
	Cuprocide 2–100	2, 3, 4, 6, 7	31	2.3	907
	Cuprocide 2–100 plus CSO ¼ per cent	2, 3, 4, 6, 7	31	3.2	878
	Bordeaux 8–6–100	2, 3, 4, 6, 7	32	0.6	885
	Bordeaux 4–3–100	2, 3, 4, 6, 7	33	1.1	870
	$ZnSO_4$ plus Hyd. L. 8–8–100	2, 3, 4, 6, 7	33	7.0	788
	Nonsprayed	———	255	40.8	554
16	Bordeaux 6–4–100	3, 5, 6, 8	161	1.2	810
	Cuprocide 1–100	3, 5, 6, 8	176	2.3	832
	Cuprocide 2–100	3, 5, 6, 8	189	1.4	805
	Cuprocide 1–100 then Bordeaux 6–4–100	3, 5, 6, 8	160	1.5	840
	Nonsprayed	———	252	33.3	568
12[d]	Copper Hydro "40" 4–100 plus CSO ¼ per cent	3, 5, 7, 8	32	1.3	652
	Cupro K 4–100 plus CSO ¼ per cent	3, 5, 7, 8	30	3.0	616
	Cuprocide 2–100 plus CSO ¼ per cent	3, 5, 7, 8	34	2.8	728
	Cuprocide 2–100 plus goulac ½–100	3, 5, 7, 8	31	1.9	707
	Cuprocide 2–100 plus rosin size ½–100	3, 5, 7, 8	31	2.7	642
	Cuprocide 2–100 plus sulfur 4–100 plus goulac ½–100	3, 5, 7, 8	33	1.4	732

TABLE 5—*Continued.*

YARD NO.	SPRAY MATERIALS[a]	APPLICATIONS[b]	NUMBER OF PLANTS	CONES AND BURS INFECTED, PER CENT	YIELD PER ACRE, LBS.[c]
		1937			
	Bordeaux 8–4–100	3, 5, 7, 8	32	1.0	740
	Bordeaux 4–2–100	3, 5, 7, 8	33	1.3	755
	Nonsprayed	———	190	51.0	388
15[d]	Cuprocide 2–100	2, 4, 6, 7	32	1.9	1,084
	Cuprocide 2–100 plus goulac ½–100	2, 4, 6, 7	30	4.0	956
	Cuprocide 2–100 plus rosin size 1–100	2, 4, 6, 7	31	4.7	896
	Cuprocide 2–100 plus CSO ¼ per cent	2, 4, 6, 7	32	2.8	978
	CSO ½ per cent	2, 4, 6, 7	31	35.6	524
	Bordeaux 6–4–100	2, 4, 6, 7	31	1.8	1,010
	Bordeaux 6–4–100	2, 6, 7	30	1.4	958
	Bordeaux 6–4–100	4, 6, 7	32	1.3	984
	Bordeaux 6–4–100	6, 7	33	4.2	792
	Nonsprayed	———	218	47.1	496
		1938			
17	Bordeaux 6–4–100	3, 4, 6, 7	68	0.0	548
	Cuprocide 1½–100	3, 4, 6, 7	62	0.2	431[f]
	Nonsprayed	———	65	5.2	372[f]
19	Copper-lime dust 25–75	2, 3, 4, 5, 7, 8	335	11.2	710
	Nonsprayed	———	339	34.7	460
2	Bordeaux 6–4–100	2, 4, 6, 7	35	1	983
	Bordeaux 6–4–100	3, 6, 7	33	2	922
	Bordeaux 6–4–100	4, 6, 7	35	4	891
	Bordeaux 6–4–100	2, 6, 7	34	5	918
	Bordeaux 6–4–100	2, 4, 6	32	18	775
	Bordeaux 6–4–100	4, 7	34	10	753
	Nonsprayed	———	33	56	534
13	Rosin-lime sulfur[g]	1, 2, 3, 5, 6, 7[h]	108	4.0	882
	Cuprocide "54" 3½–100 plus S. 6–100	1, 2, 3, 5, 6, 7[h]	110	2.1	973
	Cuprocide "54" 3½–100 plus S. 6–100	1, 2, 3, then 5, 6, 7[h]	56	2.0	1,010
	Bordeaux 8–4–100 plus S. 6–100	1, 2, 3, 5, 6, 7[h]	110	1.1	982
	Bordeaux 8–4–100 plus S. 6–100[i]	6, 7[h]	108	8.2	960
	Nonsprayed	———	54	38.4	748
1	Micronized sulfur dust	4, 5, 6, 7, 8	16	23.8	1,020
	Copper-lime dust 25–75	4, 5, 6, 7, 8	16	14.9	1,080
	Nonsprayed	———	16	57.8	780

TABLE 5.—*Concluded.*

YARD NO.	SPRAY MATERIALS[a]	APPLICATIONS[b]	NUMBER OF PLANTS	CONES AND BURS INFECTED, PER CENT	YIELD PER ACRE, LBS.[c]
		1940			
1	Micronized sulfur dust.....	4, 6, 7, 8	16	47	940
	Copper-lime dust 20–80....	4, 6, 7, 8	16	21	1,190
	Cuprocide-sulfur dust 7–93.	4, 6, 7, 8	15	17	1,255
	Bordeaux 6–4–100.....	4, 6, 8	8	2	1,640
	Bordeaux 3–2–100 plus CSO ¼ per cent.....	4, 6, 8	8	4	1,520
	Cuprocide (yellow) 1½–100	4, 6, 8	8	4	1,590
	Cuprocide (yellow) 1–100 plus SEC oil ¼ per cent..	4, 6, 8	8	5	1,520
	$ZnSO_4$ plus Hyd. L. 8–6–100	4, 6, 8	8	9	1,480
	S. 12–100.....	4, 6, 8	8	16	1,270
	Nonsprayed.....	———	17	78	612
3	S. 7–100.....	4, 6, 7, 8[i]	293	11.9	——
	Bordeaux 4–2–100.....	4, 6, 7, 8	316	1.7	——
	Bordeaux 4–2–100 plus CSO ¼ per cent.....	4, 6, 7, 8	304	1.3	——

[a]Bordeaux mixture made with hydrated lime; Hyd.L. = Hydrated lime; CSO = Cottonseed oil (edible), emulsified with goulac (sulfite lye), except when used with bordeaux; $ZnSO_4$ = $ZnSO_4$. $7H_2O$; S. = Wettable sulfur (Crown brand used in 1937–38 and Micronized after 1938). The red form of cuprous oxide (Cuprocide) was used except where Yellow Cuprocide is mentioned.

[b]Spray applications are numbered according to stage of growth of Millstate and Late Cluster varieties: 1, after second tying of vines (May 20–30); 2, vines 8 to 10 feet high (June 1–10); 3, lateral vine growth (June 11–20); 4, late June (June 21–30); 5, early blossom (July 3–10); 6, full bloom (July 11–21); 7, late bur (July 25–August 6); 8, early cone (August 7–12); 9, late cone (August 15–20).

[c]Yield of fresh hops was converted to dry weight on the basis of 75 per cent loss in weight of fresh hops when dried. The calculated number of pounds of dried hops per plant was multiplied by the number of plants per acre to give the acre yield.

[d]Growers dusted with sulfur three or four times independently of spray applications in these yards.

[e]Nonsprayed plants received considerable spray drift.

[f]Yield reduced by leafhopper injury.

[g]Formulae of rosin and lime-sulfur solutions: At applications Nos. 2 and 3, 1–2–100; at Nos. 4, 6, and 7, 0.5–0.5–100; and at No. 5, 0.375–0.375–100.

[h]Sprayed with fixed booms instead of guns at applications Nos. 2, 3, 6.

[i]Sulfur 6–100, used at application No. 6.

[j]Bordeaux 4–2–100, instead of sulfur, used at application No. 8.

The early June spray and the July sprays were the most important in effecting control.

The relative effectiveness of bordeaux 8–6–100 and red Cuprocide 3–100 applied only once was tested in a 2 acre yard. About 8 per cent of the blossoms were infected on July 20 when the sprays were applied. The grower dusted with sulfur for the control of powdery mildew twice in July and twice in August. Bordeaux was more effective than Cuprocide in protecting the cones which developed during the 34 day period after spraying (Table 6).

TABLE 6.—EFFECT OF ONE SPRAY APPLICATION IN PREVENTING BROWNING OF HOP CONES BY DOWNY MILDEW INFECTION ON "ENGLISH CLUSTER" VARIETY.

TREATMENT*	NUMBER OF GALLONS PER ACRE	DATE OF APPLICATION	DATE OF TAKING DATA	NUMBER OF CONES			CONES DISEASED, PER CENT
				Total	Healthy	Infected	
			1937				
Bordeaux 8–6–100	320	July 20	Aug. 24	1,089	930	159	14.6
Cuprocide (red) 3–100	320	July 20	Aug. 24	918	660	258	28.1
Nonsprayed	—	—	Aug. 24	814	446	368	45.2
			1938				
Bordeaux 12–8–100	350	July 27	Aug. 25	739	618	80‡	10.8
Zinc-lime 12–8–100†	350	July 27	Aug. 25	653	419	198‡	32.0
Cuprocide (red) 4–100	350	July 27	Aug. 25	761	488	222‡	29.2
Nonsprayed	—	—	Aug. 25	922	191	670‡	73.0

*Growers applied sulfur dust over all plots four times in 1937 and five times in 1938.
†Zinc sulfate ($ZnSO_4.7H_2O$) plus hydrated lime.
‡Does not include mummified burs because they were infected before sprays were applied.

1938.—The season was one of average temperature, except for short periods of high temperature in the latter parts of June and July. Rainfall was somewhat below average during May and June and above average for July and August. Infection periods were numerous and well distributed during July and August. Leaf infection was prevalent thruout the season. Infection of cones was very severe (Fig. 5).

Rosin-lime-sulfur proved less effective than bordeaux, and also injured the young tissues. Bordeaux caused slight leaf injury. Some of the increased yields following the use of bordeaux were attributable to the control of leafhoppers. As for the dusts, copper-lime was more effective than sulfur in controlling the mildew. Bordeaux 8–4–100 and lime 4–100 injured fully open blossoms when applied in the middle of the day on July 14. The distal end of practically all pistils was killed. The cones, however, appeared to develop normally in spite of this injury. Many stipules and young leaves were also browned.

The following sprays were applied on July 27: Bordeaux 12–8–100; zinc sulfate-lime 12–8–100; and red Cuprocide 4–100. Except for 2 previous and 3 subsequent sulfur dustings by the grower, no other fungicides were used. The data again indicate that bordeaux is highly effective in protecting the new (nonsprayed) growth over a pre-

harvest period of 4 weeks even in the presence of abundant inoculum and a total of 5.5 inches of rainfall (Table 6).

1939.—The 1939 season was one of moderate temperatures and sparse rainfall (Fig. 6). Infection periods were scarce until August. Infection of leaves and growing points was retarded and remained low thruout the season. Inoculum was scarce all season. Cones developed practically disease-free. The spray and dust trials, consequently, had no significance as to mildew control and so are not listed in Table 5.

It should be mentioned that leafhoppers reduced yields in many plantings. Zinc sulfate-lime (one test only) and bordeaux sprays repelled the hoppers and controlled "hopper burn" satisfactorily.

1940.—The season was characterized by low temperatures and average rainfall. Infection was sparse until July. High average temperature and lack of humid periods early in June were correlated with the light infection during the first part of this month (Fig. 7). During July, however, leaf and shoot infection progressed rapidly. The few infection periods in August permitted a portion of the unsprayed crop to mature disease-free.

Sulfur dust controlled the disease only to a slight extent. Copper-lime and Cuprocide-sulfur dusts controlled the disease somewhat better, permitting fair yields, but were less satisfactory than the copper sprays in protecting the burs and cones. Sulfur spray did not compare favorably with bordeaux or Cuprocide sprays (Table 5). No spray injury occurred.

1941.—The season was one of average temperature and light rainfall, except for a few heavy showers of short duration. Infection periods were infrequent, except for the latter part of July and the middle of August. Infection was light thruout the season (Fig. 8).

As in 1939, bordeaux was outstanding in its ability to protect plants from leafhopper injury which was particularly severe. Bordeaux 6–4–100 sprayed on July 3 at the rate of 400 gallons per acre with or without ⅛ per cent cottonseed oil injured the very young leaves. No injury appeared on plants receiving about 200 gallons per acre with fixed nozzles.

DISCUSSION OF RESULTS

A suitable spray program for a given hop yard depends greatly on (a) location with respect to air movement, (b) amount of inoculum, and (c) thoroness of spraying. Restriction of air movement thru plantings by hedges, trees, buildings, or hills leads to prolonged wet-

ting periods, early season infections, and severe epidemics requiring additional spray applications. Salmon and Ware (50) recommended that low-lying ground be avoided as a site for new hop yards. Lack of sanitation, especially with regard to basal spikes, is another condition causing early spring infection and making extra sprays necessary. Insufficient spraying of the upper leaves and vines is responsible for much of the difficulty that growers experience in controlling the disease. At least half of the liquid or dust should be directed to the upper third of the plants including the poles and twine extending above the vine tips.

Bordeaux mixture and Cuprocide have consistently given the most effective downy mildew control. Zinc oxide has been distinctly inferior. Limited tests indicate that the following materials are less effective than bordeaux: Rosin-lime sulfur, Copper Hydro "40", zinc sulfate-lime, cuprous sulfide, Cupro K, and wettable sulfurs. Bordeaux was particularly superior to other materials in preventing cone infections. Superiority over Cuprocide on cone protection was significant, tho, only in those cases where one spray application was made during the season.

A mixed program employing Cuprocide in the May and June sprayings and bordeaux for the later applications, has been as effective as the use of either material alone. This program prevented the use of bordeaux when the leaves were most susceptible to spray injury. Bordeaux should be used starting the middle of June if leafhoppers are a factor.

A spray program of four applications of bordeaux mixture 6–4–100 or of Yellow Cuprocide 1½–100 at biweekly intervals beginning the second week in June effectively controlled the disease on English Cluster varieties. For the Late and Early Cluster varieties planted in valleys, a total of 6 or 7 applications at 12 to 14 day intervals beginning the middle of May were found necessary. Bordeaux 6–4–100 was effective against both downy mildew and leafhoppers. A larger complement of lime tended to increase spray injury. Thoroly applied sprays of bordeaux 4–2–100 and 4–3–100 were as effective as the higher concentrations against downy mildew. A wettable sulfur 6–100 is added to the copper sprays in all applications during June and July to control the powdery mildew (*Sphaerotheca humuli* (DC.) Burr). Nicotine sulfate is added also when aphid control is indicated.

The addition of wettable sulfurs to copper sprays results in the formation of black copper sulfide on either or both sides of the leaf.

This occurs with bordeaux or Cuprocide sprays with or without the addition of cottonseed oil. The copper sulfide becomes evident macroscopically 3 weeks or more after spraying. This combination involves a relatively small part of the copper and sulfur residues and does not adversely affect the performance of the fungicides. In fact, the effectiveness of bordeaux or Cuprocide against downy mildew seems to be stepped up when a wettable sulfur is added to the copper spray in all applications.

The critical period for control of the disease extends from early June thru July; or the period covering the production of fertile laterals, blossoms, and young cones. Success in bringing thru a clean and full crop of cones depends primarily on the thoroness of spraying during July. If new infections take place during July, the cones of susceptible varieties will be subject to infection unless a fungicide is applied to the cones themselves.

Obtaining economical control of the disease on susceptible varieties depends a great deal on preventing the establishment of infection in the upper parts of the plants. The critical period for development of the disease has been the latter part of June and early July at which time the vines have attained over half of their growth in height and the laterals are growing out. If the vines and leaves in the upper parts of the plant become diseased at this period, the summer spore inoculum is in a position to impair the crop yield and quality. In most instances, focal spots of diseased blossoms and cones can be traced to old terminal spikes located directly over the diseased areas. In nonepidemic years, damage to cones has often been limited to vines bearing spikes near their tops. The disease can be controlled with fewer applications of sprays or dusts if infection has been kept limited to the lower few feet of vine growth thru the month of June. On the other hand, fungicidal applications, unless especially frequent and thoro, may not prevent considerable further spread of infection once the upper leaves and stems become infected.

The treatment of hop twine with a low-lime bordeaux was recently suggested by Yarwood (57) as a means of reducing infection early in the season.

Much of the crop damage by the mildew disease from the standpoint of both yield and quality occurs during August. In the period of 4 to 6 weeks between the last spray application and the end of harvest, the hop plant continues to grow. Its weight increases by at least one-third due to the production of cones. The fungicide which

protected this new growth most effectively over such a long period was home-made bordeaux mixture. This protection was probably afforded by a redistribution of some of the copper from sprayed growth to new growth during rain periods, as suggested by Salmon and Ware (47).

Rain drippings from sprayed foliage proved very toxic to the spores of the fungus. Cones borne on horizontal wires at the top of trellises often became diseased because of the lack of sufficient sprayed foliage above them. Cones picked from the tops of poles or wires in sprayed yards were diseased to a greater extent than those picked at lower levels. The reverse was true in nonsprayed yards.

Evidence that bordeaux films release copper in toxic concentrations more quickly than some other copper materials is shown by laboratory data to be published elsewhere. The superiority of bordeaux in protecting new nonsprayed growth may be due entirely to its greater tenacity and solubility.

The cumulative effect of efficient spraying over a period of years in reducing the oospore inoculum has not been studied. It is doubtful that commercial spraying alone could reduce oospore carryover and primary infection sufficiently to do more than delay the onset of serious secondary infection in epidemic years and make fewer fungicidal applications necessary. The application of fungicides would not prevent the production of oospores in basal spikes or in diseased seedlings. Theoretically, a combination of spraying, elimination of seedlings, and destruction of basal spikes could eradicate the fungus from an isolated planting.

FUNGICIDES AND MODE OF APPLICATION IN RELATION TO SIZE OF CONE

Unpublished data of Dr. James G. Horsfall, covering hop spray tests made in 1934 and 1935, show that bordeaux 8–8–100 stunted the hop cones, reducing the weight per cone by 10 to 20 per cent, while red Cuprocide and zinc oxide sprays did not stunt the cones.

Further tests on bordeaux injury were carried out by the author in 1937–41. Applications of bordeaux 8–4–100 were made biweekly thru June and July. No significant dwarfing of cones was found in 1937 or 1938, but in 1939 bordeaux reduced the average weight per cone by 23 per cent (Table 7). Cuprocide (red or yellow) caused no reduction in cone weight. The addition of cottonseed oil (1 quart per 100 gallons) to bordeaux reduced the stunting effect in 1939.

TABLE 7.—EFFECT OF CERTAIN SPRAYS ON THE WEIGHT OF MILLSTATE HOP CONES IN 1939.

SPRAY TREATMENT	NUMBER OF CONES	FRESH WEIGHT PER CONE	
		Grams	Per cent of nonsprayed
Nonsprayed	2,700	0.608 ± 0.052	100
Yellow Cuprocide 2–100	2,000	0.626 ± 0.045	103
Bordeaux 8–4–100	2,555	0.469 ± 0.050	77
Bordeaux 8–4–100 plus cottonseed oil ¼ per cent	3,000	0.586 ± 0.055	96

Hop cones of the same variety (Millstate) were not dwarfed when bordeaux mixture was applied thru fixed nozzles instead of guns (Table 8). The dosage per acre for gun spraying was between 250 to 400 gallons, according to the amount of vine growth, and that for boom spraying between 130 and 240 gallons, depending on the speed of the sprayer and whether it traveled between every row or every other row.

Bordeaux may injure young leaves, young stems, and pistils. Injured leaves are brown, shot-holed, stunted, or distorted. The use of high spray pressures and heavy applications with guns undoubtedly increase the likelihood of leaf and stem injury. Insoluble copper sprays have never been known to injure the hop plant.

The exposed portion of any pistils sprayed with bordeaux or with lime may die within 24 hours. This injury was especially pronounced when the air temperature was above 75° to 80° F at the time of spraying. The only apparent result of this injury was a reduction of seed content and smaller cones.

Reduction of pollination and lowering of the seed content result in smaller hop cones. It is estimated that seedless hops yield about 30

TABLE 8.—EFFECT OF BORDEAUX SPRAY ON SIZE OF CONES WHEN APPLICATIONS WERE MADE THRU BOOMS.

YARD NO.	TREATMENT*	NUMBER OF CONES	FRESH WEIGHT PER CONE, GRAMS
8	Nonsprayed	1,000	0.78
	Bordeaux mixture, 6–4–100	1,000	0.80
14	Nonsprayed	1,000	0.69
	Bordeaux mixture, 6–4–100	1,000	0.67

*Applications made in yard No. 8 on June 20 and July 5, 17, and 30; in yard No. 14 on July 5, 17, and 30, 1940.

per cent less than seeded hops (21). Spraying with bordeaux on hops in flower resulted in a reduction of the seed content from 2.8 to 1.1 per cent of the fresh weight (Table 9). Table 10 gives the weights of cones from yard No. 13 in 1941. The removal of staminate plants from this yard resulted in a seed content of 0.5 per cent of the fresh weight. Bordeaux spray did not stunt these "seedless" cones.

TABLE 9.—EFFECT OF BORDEAUX SPRAY ON SEED CONTENT OF MILLSTATE CONES.

TREATMENT*	NUMBER OF CONES	FRESH WEIGHT OF CONES, GRAMS	WEIGHT OF SEEDS†	
			Grams total	Per cent of cones
Nonsprayed	1,000	592	16.5	2.8
Bordeaux 6–4–100	1,000	534	5.9	1.1

*Applications made on June 28 and July 10 and 27, 1940.
†Seeds separated from oven-dried cones.

Another point to be considered here is the tendency of the hop plant to produce larger cones when its normal complement of fruit has been reduced by disease or other factors.

The available evidence indicates that certain alkaline sprays stunt hop cones and that the most important causative factor is the blossom injury that results in a more or less seedless cone. The enhanced market value of seedless hops may offset the loss in weight due to the stunting of cones by bordeaux. The possibility of preventing the dwarfing of cones by not spraying with bordeaux during the 3 weeks of blossoming has not been investigated.

RESISTANT VARIETIES

The use of resistant varieties is a promising method of downy mildew control. Much of the value of hops, however, depends upon intrinsic qualities, and to establish the commercial possibilities and

TABLE 10.—EFFECT OF BORDEAUX SPRAY ON FRESH WEIGHT OF "SEEDLESS" CONES OF MILLSTATE VARIETY.

TREATMENT*	NUMBER OF CONES	WEIGHT PER CONE, GRAMS
Nonsprayed	1,000	0.60
Bordeaux 6–4–100	1,000	0.59
Bordeaux 6–4–100 + ¼ per cent cottonseed oil	1,000	0.62
Yellow Cuprocide 2–100	1,000	0.59

*All treatments included sulfur 4–100 and nicotine sulfate; applications made on July 3, 15, and 29, 1941.

suitabilities of a new or untried variety requires many years. Ultimately, the disease may be controlled chiefly by the use of resistant hops that are now being developed and tested at several stations in this country and Europe.

Except in severe epidemic years and in certain low-lying situations, the more resistant introduced varieties may now be grown in this State with little trouble from downy mildew. Brewer's Gold and Fillpocket are examples of these new varieties. All present-day commercial varieties, including those just named, have proved to be more or less susceptible, however. Certain varieties, notably the Fuggle, reported at first to be immune, later proved to be slightly susceptible (49). Any resistant hop, staminate or pistillate, may be of immediate value in the development of new varieties.

A varietal test planting was established in Waterville, N. Y., in 1937. Downy mildew was encouraged here for the express purpose of comparing varietal resistance. Records have been kept on all varieties as to the resistance of their leaves, stems, and cones. Cone resistance is the important feature commercially. The data for 1940 (Table 11) indicate that those varieties with high resistance to cone infection tend also to have a high resistance to basal spiking and leaf infection. Less complete data for 1938 and 1941 show the same tendency.

If susceptibility to cone infection is correlated with susceptibility

Table 11.—Relative Susceptibility of Certain Hop Varieties to Downy Mildew, Waterville, N. Y., 1940.

Variety	Number of plants	Per cent of cones diseased	Number of spikes per hill	Per cent of hills spiked	Resistance of leaves*
Early Cluster	31	90	1.3	58	0
Late Cluster	56	89	1.2	41	0
Millstate	39	64	1.9	38	0
Cat's-tails†	15	49	1.6	47	0
OD31†	14	48	0.9	36	0
Brewer's Favorite†	15	47	0.5	33	+
219†	5	23	4.0	100	0
R1/9†	15	16	0.4	27	0
OG83†	7	14	0.7	29	0
OI47†	13	10	0.0	0	++
Bullion†	16	9	0.2	6	+++
Early Promise†	4	5	0.5	25	+
Brewer's Gold†	19	4	0.6	16	++
Fillpocket†	11	3	0.0	0	+++
HH44†	4	2	0.0	0	++
Fuggles	33	1	0.0	0	+++

*Rated from susceptible (0) to very resistant (+++).
†Varieties developed by Prof. E. S. Salmon.

to spiking and leaf infection, the problem of breeding resistant varieties will be simplified and speeded up as seedlings could be tested in their first year and all those showing leaf or shoot infections discarded. It would be unnecessary to hold them 3 or 4 years in order to determine cone resistance. It is possible to grow and test several batches of seedlings in succession each year in greenhouse and field.

RECOMMENDATIONS FOR CONTROL

No single program will solve all the problems of controlling downy mildew on hops as they are encountered in different seasons and in different localities. The following recommendations are meant to be used merely as a guide in selecting suitable control practices for any one planting or season.

CULTURAL PRACTICES

The most important single practice to keep down sources of mildew in hop plantings has proved to be the frequent removal and destruction of basal spikes *before sporulation occurs*. Much infection is prevented by removing the extra shoots and stripping leaves and lateral vines from the lower parts of the vines. The extra shoots ("suckers") must be removed often enough to keep them from falling over on the soil.

Reduction of primary infection can be obtained by limiting the production and carry-over of oospores and by treatment of the soil to prevent their germination. The incidence of primary infection has been lower in those yards that were sprayed with fungicides during the previous season than in similar unsprayed plots. Obviously, fewer oospores are produced on sprayed plants. Likewise, fewer oospores will be incorporated in the soil if the infected vines cut off at harvest are hauled off the yard immediately and burned when dry.

Treatment of the soil over the crowns with chemicals, such as calcium cyanamide, has been effective in reducing the number of basal spikes. Crown treatments, however, have not obviated the need for roguing basal spikes.

Crown treatments as well as sanitary practices may be advisable in certain poorly sprayed yards where spiking tends to be so serious that it is occasionally difficult to find enough healthy shoots in any one hill for training.

Modification of certain practices in the culture of hops will avoid much of the infection. Most of these modifications entail no additional

expenditure of labor or money. The following practices are suggested:

1. Thoroly prune the crowns before growth commences in the spring, thereby removing the source of many unwanted shoots which might otherwise become spiked. Besides removal of rhizomes, the top of each crown should be cut back below the level of the soil, leaving one or two rows of buds.
2. Train the young vines early and often enough to keep them from touching the soil.
3. Reduce the number of vines per hill to a point consistent with maximum production. Fewer vines result in better movement of air and in the opportunity to spray more thoroly.
4. Provide for better distribution of vine growth so that crowding is prevented. "Housing-in" of growth predisposes to infection and makes thoro spraying difficult.
5. Space hills further apart to provide for freer movement of air thru the yard.
6. Destroy escaped or "wild" hop plants in the neighborhood of cultivated plants.
7. Remove basal spikes before carrying out other operations, such as training, suckering, and stripping. Hop vines should never be touched when the plants are wet if disease is present in the yard.
8. Place vine supports so as to facilitate the application of sprays.

Replantings of missing hills in established yards should be made with vigorous 1- or 2-year-old "sets" instead of rhizome cuttings because the latter put forth slowly growing shoots that are commonly killed in oospore-infested soil. New plantings on land in which hops have grown within 2 or 3 years should also be made with sets.

SPRAYING AND DUSTING

In most New York plantings, it is possible to control the downy mildew of hops by spraying alone. More certain and more economical control is obtained, however, by first supplementing the spray program with the sanitary practices outlined above.

Bordeaux mixture has given the best disease control of any material tested. In addition to controlling the disease, it very effectively repelled leafhoppers so it is considered indispensable in yards where the insects are prevalent. Yellow Cuprocide 1½–100 can be used in yards where the insects are not harmful. Yellow Cuprocide caused no injury to the hop plant, but it was less effective than bordeaux in protecting unsprayed parts of the plants. Bordeaux mixture 4–3–100 when applied thoroly was as effective as the 6–4–100 formula. In the average season each acre of bearing hops should receive at least 1000 gallons of spray mixture. At least 350 gallons of the total should be applied at the last spraying when the cones begin to form.

Dusting may be used as an adjunct to the spray program. Either copper-lime dust, 25–75, or Cuprocide-sulfur dust, 7–93, may be applied during August when spraying would stain the cones. Two or three dust applications should be made in valley yards during the first half of August to protect the upper cones in wet seasons. Dusting is also valuable as a stop-gap to check an imminent epidemic outbreak until spraying can be completed. In a commercial planting, copper-lime dust, 25–75, applied weekly during June and July under extremely epidemic conditions, controlled the downy mildew disease but did not control leaf hoppers.

Methods of applying fungicides against downy mildew of hops deserve careful attention. Dusts should be blown up thru the leaves with more than enough force to reach the highest vines. Dusts should be applied when the leaves are wet on both surfaces and when the air is still. Sprays may be applied thru hand-directed guns or brooms or thru fixed nozzles (boom). In either case the major portion of the spray should be directed to the upper half of the vines and especially to the tops. The twine and poles above the growing shoot tips should be covered with the spray also. A pressure of about 350 pounds is most satisfactory. Pump capacity should be sufficient to spray over the vine tops.

The spray program for bordeaux and Cuprocide should consist of four treatments, applied at approximately 2-week intervals (a) when the vines are about 8 feet high; (b) 2 weeks later, or about June 24; (c) at the beginning of full blossom (bur), or about July 11; and (d) at the beginning of cone formation. With early varieties, this program should be begun and ended about 2 weeks earlier than is indicated above. The very susceptible varieties, Early and Late Clusters, planted in valleys, have required as many as 8 applications of bordeaux applied at 7- to 10-day intervals for satisfactory control during severe epidemics. With these varieties, apply the first spray 2 weeks after the first spikes appear.

A reduced program of two or three applications, starting the latter part of June, will be effective in dry seasons. Regardless of lack of disease development during June, the two July applications should never be omitted because of the danger of cone infection.

New plantings are often seriously weakened or fail entirely because of defoliation and killing of terminal growth. Cultural methods used in the first year of growth favor disease development. The practice of twisting the vines of susceptible varieties around the marking stakes

makes disease control by any means practically impossible. Young plants should be dusted with copper-lime, 25–75, or sprayed with Yellow Cuprocide, 1½–100, at 2-week intervals thru the season beginning with the first sign of infection. Both spraying and dusting have effectively protected young plants in experimental plantings during the past 4 years.

RESISTANT VARIETIES

Resistant varieties that prove to be of high quality and acceptable to both the brewer and the producer may be grown in place of the susceptible Cluster varieties. Brewer's Gold is fairly resistant and appears to be acceptable. Growers with small plantings should grow one or more resistant varieties such as Brewer's Gold, especially if their yards are subject to epidemics and adequate spraying equipment is not available. In most seasons, downy mildew can be controlled on the more resistant sorts with one application of bordeaux to protect the bur and cones. This is applied about 7 days after the beginning of the blossoming or bur period.

SUMMARY AND CONCLUSIONS

The downy mildew (*Pseudoperonospora humuli* (Miy. and Tak.) Wils.) is the most destructive disease of hops in New York State. It reduces the quality of the crop as well as the yield. Investigations were conducted from 1937 to 1941 with the purpose of increasing knowledge of the epidemiology of the disease and applying this information to the problems of control.

The maximum, minimum, and optimum temperatures for sporangial germination were, respectively, 28°, 5°, and 15° to 20° C. Sporangia germinated to form zoospores in about 1 hour at optimum temperatures. The zoospores also germinated in about 1 hour at these temperatures. Sporangia on leaves survived 3 to 4 week periods of severe drying but were very short-lived after separation from the leaves. Zoospores proved extremely susceptible to desiccation. Their maximum period of motility in water containing hop leaf tissue varied from 2 days at 20° to 5 days at 10° C. Their germination and period of activity were greatly reduced in the absence of hop leaves. Oospores survived 30 months of dry storage in the laboratory and a similar period at 0° F.

Experiments on the relation of certain environmental factors to infection in the greenhouse are reported. The shortest periods of

continuous wetting that permitted infection of hop leaves by sporangia at 24°, 18°, 13°, and 10° C were 1½, 2, 4, and 6 hours, respectively. Heaviest infection occurred at 13° to 18° after 24 hours in the inoculation chamber. The optimum temperature range for spore germination is also optimum for infection of the host plant.

Bordeaux and rosin-lime-sulfur sprays applied after inoculation were relatively ineffective in checking infection in its initial stages. Sulfur sprays and dusts inhibited sporulation on plants under bell jars but not in the field.

Older leaves proved much more resistant to infection than young leaves. Leaves produced at higher temperatures were more resistant than those produced at lower temperatures. Inoculated greenhouse plants subjected to 24 hours of severe drying before the infection period were not infected. Oospores infected stems, leaves, seedlings, and buds on crowns and rhizomes of greenhouse plants.

Perennial growth (rhizomes and crown) of Early and Late Cluster varieties became infected and was sometimes killed on unsprayed plants in experimental plantings, but rarely on sprayed ones.

The development of epidemics is discussed. Cultivated and escaped hops are the only plants infected by *Pseudoperonospora humuli* in this State. Under New York conditions, the hop downy mildew fungus has been found to overwinter only in the form of oospores produced in diseased stems, leaves, cones, and seedlings thruout the growing season. These "resting" spores are abundantly incorporated in the soils of most hop yards, and some oospores do not germinate until 2 years after their formation.

The systemic infection of young shoots by oospores results in the formation of "basal spikes" and coincides approximately with the beginning of the host's growth. These basal spikes continue to appear over a period of at least 5 weeks and they initiate the production of secondary inoculum (sporangia) within 2 to 3 weeks after the appearance of growth each spring. The production of sporangia occurs thruout the entire growing season on all infected parts of the hop plant above ground. This production depends especially upon a high relative humidity at night. Prolonged periods of hot dry weather reduce the population of sporangia, but never completely eliminate them; so viable spores are always present to be spread by wind, rain, and the workers who train the hop vines. As the vines grow to their full height, forming new susceptible tissue thruout the season, secondary infection, starting at the base of the plant, becomes established

progressively higher and the disease assumes epidemic proportions during prolonged rainy periods of June, July, or August.

The important factor in the development of epidemics is the frequency of infection periods between late May and mid-August. Other factors, e.g. availability of inoculum, susceptible tissue, night periods of high humidity, and a favorable temperature, have been seldom or never limiting factors in the rapid spread of the disease.

Control experiments were carried out in the epidemic years of 1937, 1938, and 1940, and in the nonepidemic years of 1936, 1939, and 1941. Control recommendations are given.

Sanitation is an important adjunct to spraying, especially in low-lying sites. The most important practices, designed to reduce secondary inoculum in May and June when growth is too rapid for economical control by spraying alone, are (a) elimination of basal spikes before they sporulate, and (b) frequent pulling of extra growth ("suckers") at the bases of the plants.

New plantings should be made in fields with enough wind sweep and air drainage to dry the plants quickly after rains or dews. Epidemic outbreaks may be avoided to some extent in established plantings by removing nearby hedge rows and trees, training fewer vines, providing better distribution of vine growth, stripping the first few feet of vines, and destroying escaped hops within a mile of the yards.

Bordeaux and Yellow Cuprocide gave the most effective control of the copper, zinc, and sulfur materials tested. An effective program of spraying for most hop yards in this State consists of four biweekly applications of bordeaux 6–4–100 or Yellow Cuprocide 1½–100 beginning early in June. Dusting with copper-lime, 25–75, or Cuprocide-sulfur, 7–93, is a useful addition to spraying when fungicides must be applied to the cones and when epidemic outbreaks require immediate attention. The performance of the bordeaux and Cuprocide sprays was not improved by any of the spray amendments tested, except cottonseed oil.

Mildew infection of new unsprayed growth on bordeaux-sprayed plants was low compared to infection of similar growth on plants sprayed with other copper or zinc materials. Home-made bordeaux spray tends to protect the new growth between sprays, presumably due to the redistribution of soluble copper.

Bordeaux may injure young tissues of the hop plant and stunt the hop cones. These effects have been observed only when the spray was applied thru guns at the rate of about 400 gallons per acre. Com-

mercial spraying thru fixed nozzles at a lower gallonage has produced no injury or stunting. Zinc oxide may cause necrotic lesions on leaves. Leaf injury by bordeaux and zinc oxide was reduced by adding ¼ per cent of cottonseed oil to the sprays. Insoluble copper spray materials did not cause injury. Cone stunting by the bordeaux spray appears to be caused to a great extent by a lowering of the seed content thru killing of pistils.

A report is given on comparative resistance of hop varieties to downy mildew infection and the importance of varietal resistance in the control program indicated.

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